RESPONSES TO SALINITY CHANGE AS A TIDAL TRANSPORT MECHANISM OF PINK SHRIMP, *PENAEUS DUORARUM* [1]

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Many species of penaeid shrimp carry out extensive movements during the course of a life cycle. Larval and post-larval stages may travel from offshore spawning sites to inshore nursery areas, frequently deep into estuaries or mangrove swamps where they remain until they return to offshore waters as juveniles or sub-adults. This investigation is concerned with the method whereby the postlarvae and juveniles of *Penaeus duorarum* Burkenroad carry out their respective movements into and out of nursery areas.

Off southern Florida spawning in this species occurs in the vicinity of the Tortugas shrimp fishery grounds approximately 60 to 100 miles S.E. of the Everglades (Munro *et al.* MS). The early postlarval stages (total length 0.8 to 1.4 cm) arrive in the estuary where they remain until they return to deeper waters as juveniles or subadults (t. l. approximately 7.0 to 10.0 cm). Sampling data (Tabb *et al.*, 1962; Hughes MS) show clearly that the arriving postlarvae are predominantly collected from night flood tides while the juveniles are taken on the night ebb tides. This observation agrees with that of St. Amant *et al.* (1966) for the brown shrimp, *Penaeus aztecus* Ives, the postlarvae of which move into Louisiana estuaries principally on flood tides.

By selective use of tidal currents as transporting media the movements of animals into and out of inshore waters are facilitated and the position of certain species within such areas maintained (reviews, Verwey, 1958, 1960; Stieve, 1961). In the few experimental investigations of these movements it has been found that some physical or chemical change associated with the change in tide elicits a corresponding behavioral change, enabling the animal to utilize one or other tide for its displacement while avoiding displacement by the alternate tide (Creutzberg, 1961; Haskins, 1964).

In the inshore waters usually occupied by penaeid shrimp the factor which changes most with change of tide is salinity. In the canal from which the material for this study was collected, salinity changes between tides were seldom less than 5‰ and in summer were frequently greater than 10‰. On the supposition, therefore, that responses to salinity changes may contribute to the tidal transport mechanism, they were investigated in both postlarvae and juveniles.

METHODS AND APPARATUS

All shrimp were colleced at night from Buttonwood Canal in the estuary. Discovery-type plankton nets were suspended from a bridge into the strong tidal currents. Depending on the season and the state of the tide, it was possible to

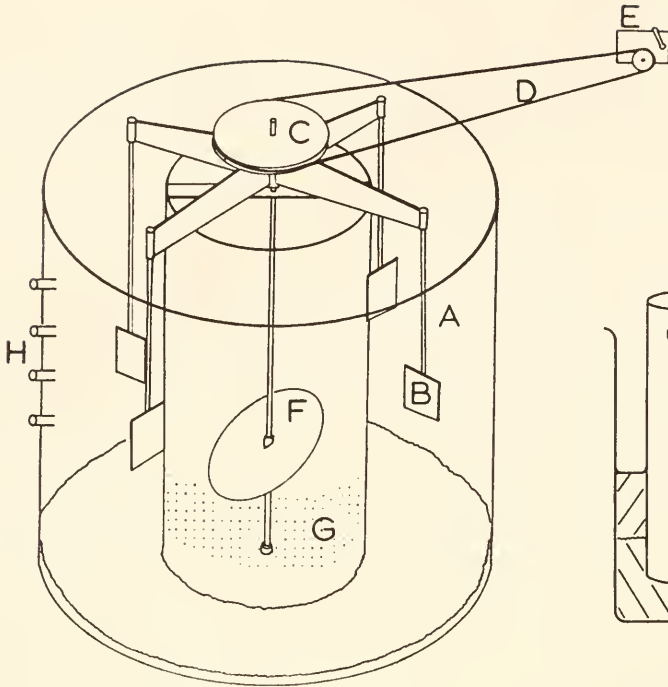FIGURE 1.   FIGURE 2.

FIGURE 1.   Current chamber.   For details see text.
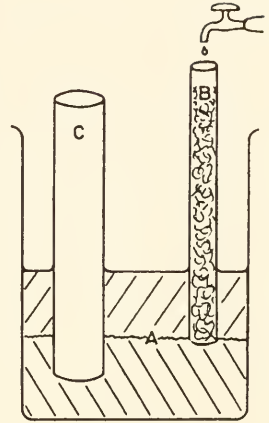FIGURE 2.   Apparatus to investigate perception of salinity differences by postlarvae.   For details see text.

collect several hundred postlarvae or upwards of five juveniles in each net during a ten-minute haul.   The shrimp were placed in five-gallon jars and taken immediately to the laboratory.   Two types of apparatus were used.

1.   A current chamber (Fig. 1), a modification of that used by Creutzberg in studying eels (1961).   Two "Plexiglas" cylinders were set, one within the other to form a circular canal between them (A).   A current was created within the canal by means of four paddles (B) attached to a central pulley (C) connected by a rubber drive belt (D) to a variable speed motor (E).   Reductions in the salinity of the water of the canal were effected by running distilled water into the inner cylinder where it was mixed by an angled disc (F) attached to the central pulley and allowed to penetrate the canal through numerous small holes (G).   Salinity was monitored at regular intervals from water siphoned from a level within the chamber approximately where the shrimp were swimming.   The bottom of the canal was covered with 5 cm of beach sand, and the water level was altered and maintained by a series of outflow points (H).   The entire apparatus was housed in a light-tight enclosure and illuminated by day by a 150 w flood lamp, the beam from which was diffused by deflection off the white roof of the enclosure.   A 10 w red bulb, casting only enough light to permit observation at night, was suspended over the center of the apparatus and kept on constantly.

2. The perception of salinity differences was investigated in a simple apparatus (Fig. 2) in which a discontinuity barrier (A) could be created between bodies of water of differing salinity. Water was run to a depth of 3 cm in a 500-ml beaker. Onto the surface of this, water of lower salinity was slowly run through a tube filled with cottonwool and sand (B), which prevented turbulence. Effective barriers were thus formed between waters differing in salinity by only 1‰. Postlarval shrimp were introduced through a second tube (C) directly into the water of higher salinity, and their reactions to the discontinuity barrier were observed and recorded. Dyeing techniques in one or other bodies of water showed that the barrier was not rapidly broken down, even when frequently penetrated by swimming postlarvae.

Results

Experiments in the current chamber were generally conducted on newly caught specimens, although occasionally material which had been in the laboratory for a week or more was used. Seven (Series I) or eight (Series II) shrimp were placed
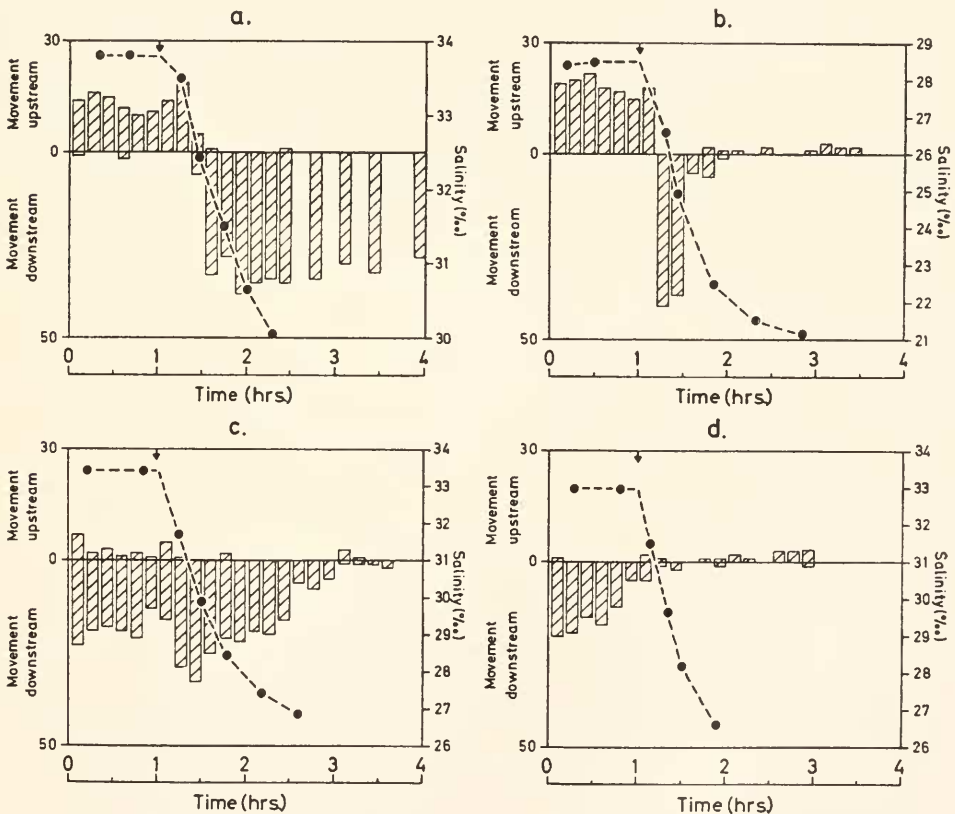

Figure 3. The effect of a decrease in salinity on the swimming of juveniles. Salinity is indicated by the broken line and the time of onset of the decrease by the arrow. For further explanation see text.

in the apparatus at one time.   The salinity of the water was between 28‰ and 34‰.
The current was maintained at 12 cm/sec.   This was arbitrarily chosen as a speed
against which the shrimp could swim but which did not erode the substrate.   The
direction and extent of swimming of the shrimp were recorded at intervals of 10
or 20 minutes for several hours before imposing a salinity decrease, and for up to
4 hours following the decrease.

Responses of juveniles

Juvenile shrimp maintained in currents of water usually orientate and actively
swim upstream.   However, when they are deprived of food for a few days or when
they are in polluted water, downstream swimming occurs.   In addition, downstream
swimming sometimes takes place in the apparent absence of any environmental
change.   These apparently spontaneous reversals in sign of rheotaxis are the sub-
ject of another paper (Hughes, in preparation).

In these experiments there was usually a conspicuous change in behavior follow-
ing a decrease in salinity within the current chamber.   If swimming against the
current the shrimp turned and swam downstream (Fig. 3a, b), or if they were
already swimming downstream they increased the speed of downstream swimming
(Fig. 3c).   There were a few exceptions to this (Fig. 3d), apparently when the
salinity decrease was imposed towards the end of the downstream swimming phase.
This active swimming sometimes persisted for several hours, or for less than an
hour.   The more rapidly the salinity was decreased the more marked was the
response of the shrimp.   A slow reduction in salinity (2‰ in 40 min) failed to
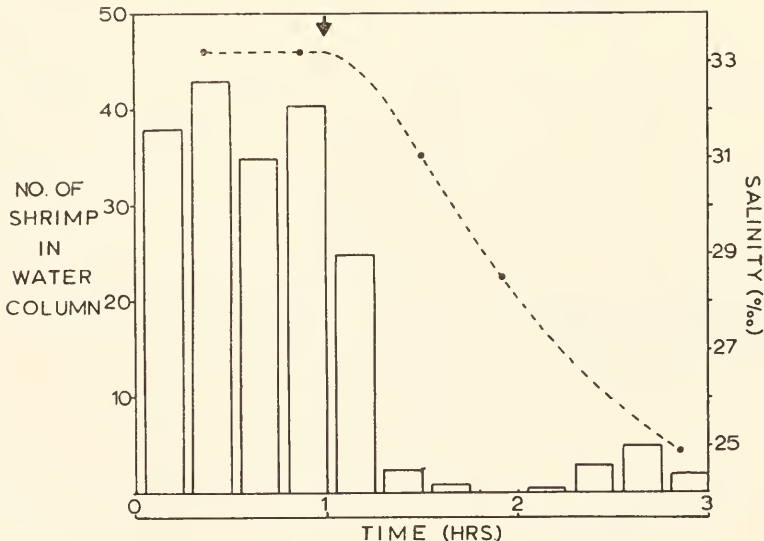elicit the response produced by the same reduction taking place in 20 min.   A

Figure 4.   The effect of a decrease in salinity on the occurrence of postlarvae within the
water column.   Salinity is indicated by the broken line and the time of onset of the decrease by
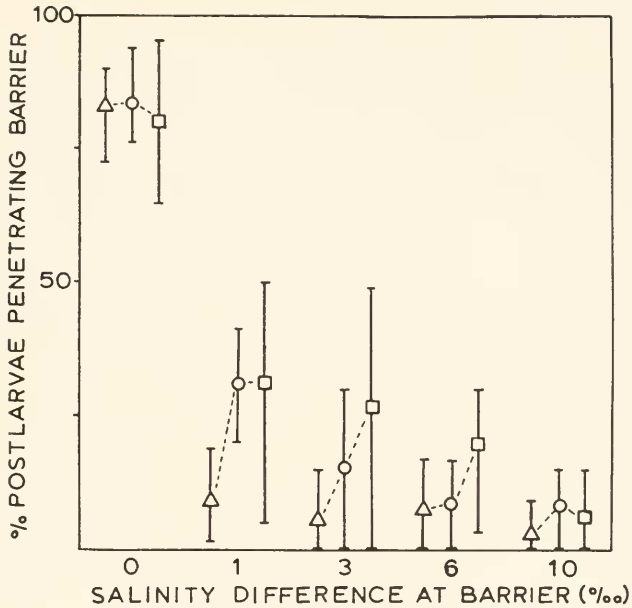the arrow.

FIGURE 5. The responses of postlarvae at salinity discontinuity barriers of various magnitude. The figure indicates the extent of penetration of the barrier during the first ($\triangle$), second ($\bigcirc$) and third ($\square$) five-minute period following exposure to it. In each case the mean of three experiments is given; the vertical lines indicate the range.

greater (10–15‰) and more rapid decrease was required to elicit this behavior in shrimp which (for reasons stated above) had swum downstream earlier in the night or which had been held in the laboratory for a few weeks. In these cases, downstream swimming, once elicited, was usually of short duration (less than 30 min).

The consistency and predictability of the variation in response suggests a "changing responsiveness" to the stimulus of salinity decrease. This was not critically examined and remains supposition.

Responses of postlarvae

Similar salinity changes were imposed on postlarvae. The current speed was maintained at 5 cm/sec, a velocity against which the smaller animals could swim.

A salinity decrease of 2 to 3‰ caused them to drop out of the water column and confine their activity to the substrate and the water just above it (Fig. 4).

In an earlier report (Hughes, MS) it was stated that a decrease in salinity caused a decrease in activity of postlarval pink shrimp. Although in subsequent experiments this was sometimes the case, it was by no means invariable: frequently the shrimp remained active on and just above the substrate.

Results were not always consistent; at times a greater decrease was required before the postlarvae would drop out of the water column. Again it is possible that a rhythm controlling the responsiveness to salinity decrease is present. This merits future investigation.

The perception of salinity differences by postlarvae

From previous experiments it was apparent that both juvenile and postlarval shrimp would perceive and respond to changes in salinity as small as 2‰ or 3‰. In the case of postlarvae this was verified and further defined by experiments conducted in the apparatus in which a discontinuity barrier was created between bodies of water differing in salinity. Prior to the experiments the postlarvae were kept in water of 33‰ for 24 hours. Ten individuals were then placed into water, also of 33‰, in the apparatus (Fig. 2), and their responses were recorded at the barrier between this water and bodies of water of 23‰, 27‰, 30‰, and 32‰. Normally postlarvae placed in a beaker swim up and down within the water column, but in this apparatus after penetrating the barrier they would usually sink motionless to the bottom before again swimming upwards.

Control experiments, in which no barrier was present, were also conducted. The results (Fig. 5) clearly indicate that the barrier is perceived even when the salinity difference is as low as 1‰. Usually after repeated contacts the shrimp penetrated the barrier and ultimately swam on either side of it. The increased incidence of penetration during each successive five-minute period (Fig. 5) is a result of these repeated contacts. Lance (1962) in her study of the responses of a number of zooplankters to salinity discontinuity barriers, recorded similar sinking to the substrate following penetration of low salinity water. She also found that
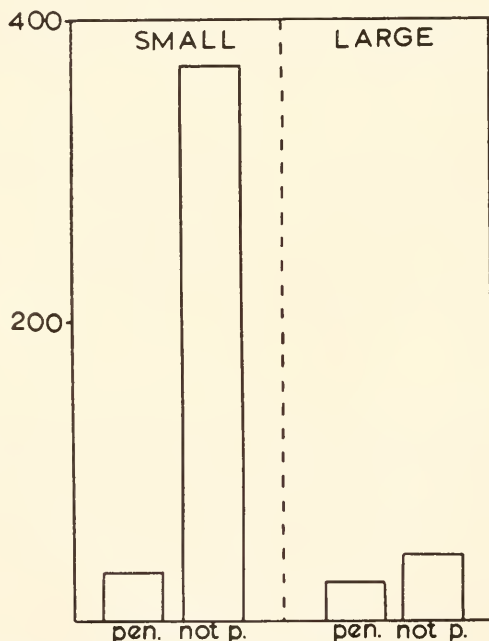

FIGURE 6. A comparison of the responses of "small" and "large" postlarvae at a discontinuity barrier (4‰ difference). The bars represent the total postlarvae which, during three separate fifteen minute trials penetrated (pen.) or, having swum up to the barrier, did not penetrate (not p.) it.

after a period of exposure to any particular salinity the number of animals swimming in the upper half of each diluted column progressively increased during the course of the experiment.

The dependence on postlarval size

In the foregoing experiments it appeared that the behavior of the postlarvae at the discontinuity barrier was dependent on their size to some extent. This supposition was tested by comparing the responses of two size-groups, each comprised of 12 individuals, at a barrier between waters of 34‰ and 30‰. The experiment was repeated three times using fresh groups of animals.

The postlarvae were selected arbitrarily as "small" or "large." In the first experiment each animal was measured and rostral spine counts taken. The "small" postlarvae ranged in total length from 9.2 to 11.1 mm (mean 9.8) with a mean rostral count of 6. The "large" ranged between 11.5 and 13.1 mm (mean 12.2) with a mean spine count of 8. Records of growth in the laboratory indicated that these size differences represented approximately a week's growth. In the following two experiments the criteria for the sizes were the same as in the first experiment.

The results (Fig. 6) are expressed as the total number of postlarvae which, on reaching the barrier, penetrated or failed to penetrate it during a 15-minute period. These show clearly that smaller postlarvae are less likely to penetrate the barrier than their larger counterparts, and that they are, in addition, more active.

DISCUSSION

Investigations of the responses of both postlarval and juvenile shrimp to changes in salinity suggested a mechanism whereby the tide-associated movements may be carried out by this species.

Juveniles

Juvenile shrimp habitually orientate into and actively swim against a current but it was found that a relatively small salinity decrease (2 to 3‰) was sufficient to reverse the sign of the rheotaxis, causing them to turn about and swim downstream. The downstream swimming often gave way to passive drifting with the current which could continue for four to five hours in the experimental situation.

Upstream and downstream swimming differs in a manner which is certainly highly adaptive. Upstream swimming occurred as a series of short "hops" close to the substrate with constant maintenance of orientation by returning to the substrate, whereas downstream swimming occurred at varying depths in the water column and without constant reference to the substrate. In the experimental situation the proximity of the walls, the substrate, and the movement of the paddles could provide reference points outside the current enabling downstream orientation. But in nature, with greater depths, current speed and turbulence, the shrimp, having lost contact with the substrate would not be able to orientate at night, but would be passively displaced by the prevailing ebb tide. Even in the current chamber active downstream swimming gave way to passive drifting sometimes for hours. In all probability the juvenile shrimp taken in ebb tide samples are not orientated down-

stream but are being passively displaced, perhaps following an initial period of downstream swimming. (The marked downstream orientation which initially followed a salinity decrease indicated a clear reversal in the sign of the rheotaxis, and not merely a suppression of the positive orientation to current.)

The occurrence and duration of downstream swimming depended on the magnitude and rate of salinity decrease, the time the shrimp had been maintained in the laboratory, and their swimming behavior prior to the decrease. However, the consistency of the response and the predictability of its modifications suggested a periodically changing responsiveness to the salinity decrease. And on the basis of the many occasions in which downstream swimming persisted long after the changes had ceased, it seems possible that the decrease was only the "trigger" releasing downstream swimming. These points were not critically examined and remain supposition. It is evident, however, that in an estuarine environment, where frequent fluctuations in salinity occur, there would be adaptive advantage in temporarily synchronizing downstream swimming with the time of the ebb tide.

Reversals of rheotactic response have been little investigated, but precedents do occur in the literature. Creutzberg (1961) working on the elver, *Anguilla anguilla* L., found a reversal similar to that described here. He showed that elvers would swim against a current containing (p. 336) "an attractive substance, . . . which is presumably an odor specific to inland water," but that when this "odor" was decreased they would swim with the current. Thus in nature they would swim inshore with the flood tide, but avoid displacement by swimming against the ebb. Keenleyside and Hoar (1954) showed that increases in temperature caused reversals of rheotaxis in three species of juvenile salmon, and a temperature increase of 5° C was shown by Beauchamp (1937) to induce a positive rheotaxis in the turbellarian *Planaria alpina.*

Postlarvae

Experiments which tested postlarval responses at discontinuity barriers between waters of different salinities showed clearly an ability to perceive and respond to a difference of as little as 1‰. In water of higher salinity (such as normal seawater) the postlarvae are active in the water column. If, however, the water becomes stratified with water of lower salinity run onto its surface, the shrimp are confined nearer the substrate through an apparent "reluctance" to penetrate the less saline water. This dropping to the substrate was therefore not, as had been previously suggested (Hughes, MS), merely a reduction in activity similar to that reported by Lance (1962) for zooplankters moving into regions of diluted sea water, but indicated an "aversion" to penetrating the water of lower salinity. Clearly these reactions in nature would limit displacement to the time of the flood tide. In normal sea water the postlarval shrimp are active in the water column and, being incapable of withstanding even slow currents they would be displaced by the prevailing tide. With decrease in salinity during the ebb tide the postlarvae are excluded from the water column and remain on or near the substrate where they are better able to maintain position and are less readily displaced.

The marked "aversion" for waters of lower salinity and the high level of swimming activity exhibited by "small" postlarvae become considerably reduced within a period of approximately one week. It is probable that these changes occur at a

time when the original response is no longer necessary. Sampling data (Tabb *et al.*, 1962) from two points three miles apart along a canal leading into the Everglades indicate that postlarvae may be transported this distance in only one flood tide, and that the larvae may therefore penetrate deeply into estuaries within only a few days of their arrival in inshore waters.

A similar effect of salinity change on activity probably maintains oyster larvae within inshore waters (Haskins, 1964), and Lance (1962) showed that a number of zooplankters were restricted to certain ranges of salinity in stratified estuaries by their responses to discontinuity barriers, suggesting (p. 131) that "discontinuity layers will influence the dispersal of zooplankton by modifying the position of individuals relative to prevailing water currents." Further, Grindley (1964) confirms that low salinity surface waters in an estuary (River Test, England) prevented most species of estuarine zooplankton from upward movement. He also showed experimentally that under the same conditions the copepod *Pseudodiaptomus hessei* (Mrázek) was prevented from carrying out its normal vertical migration and confined instead to deeper layers.

The tidal transport mechanism—Summary

The method whereby responses to salinity changes occurring with changes in tide may facilitate the respective displacements of postlarval shrimp into and out of inshore nursery areas is summarized as follows. In the case of juvenile shrimp a positive rheotaxis is present throughout flood tides when "normal" sea water salinities prevail, but when salinity decreases during ebb tides the sign of the rheotaxis is reversed and downstream swimming occurs. Thus in nature juveniles will be moving offshore during both flood and ebb tides, swimming in a series of short "hops" against even very strong flood currents (earlier experiments have confirmed this ability) and swimming or being passively displaced with the ebb tide.

Postlarvae within the water column are readily displaced by currents. The rise in salinity occurring with the flood tide causes them to be active in the water column and therefore to be transported inshore. Decreased salinity during the ebb causes them to reduce activity or confine it to deeper layers near the substrate, from where they are better able to withstand the offshore current.

It is not meant to be suggested that salinity changes are the only stimuli inducing appropriate behavioral changes since other aspects of "water quality" may operate similarly. The results do show, however, that salinity changes in the experimental situation elicit responses which, if they are the same in nature, would lead to the type of tide-associated movements which are observed.

That other factors may operate is suggested from records such as those of Champion (pers. comm.) and Slack-Smith (MS) showing that large numbers of juvenile shrimp are present in estuaries (St. Lucia, South Africa and Shark River, Western Australia, respectively) in which the salinities are higher than in the open sea, rising in both to over 60‰. Presumably the shrimp are able to leave these estuaries. It is possible that both postlarvae and juveniles respond similarly to salinities that are either much higher, or lower than normal sea water. If this is the case then rheotaxis of juveniles would be reversed in the presence of increased salinity, causing them to swim downstream during the ebb, and the inshore move-

ment of the postlarvae would be facilitated by an "aversion" to the very high salinities of the ebb similar to that shown to low salinities.

Rainfall—commercial shrimp catch correlations

These results offer a probable explanation for the marked positive correlations reported by Hildebrand and Gunter (1952) and Gunter and Hildebrand (1954) between the commercial catches of *Penaeus setiferus* (L.) off the coast of Texas and the rainfall of the previous year, and similarly between catches of *P. duorarum* and Florida rainfall of the previous year (Iversen, unpublished). Obviously salinity differences between tides would be consistently greater with increase in freshwater runoff. This would facilitate both the movements of postlarvae and juveniles. It is probable that the records of Tabb *et al.* (1962), showing that large juvenile pink shrimp remain in inshore waters when the salinity within the everglades rises to 30‰, are evidence of the breakdown of the tidal transport mechanism in the absence of the usual salinity differences between the tides.

Summary

1. The inshore movements of postlarval pink shrimp and the subsequent offshore movements of the juveniles are facilitated by flood and ebb tides, respectively. This investigation concerns the behavioral mechanisms involved in the selective use of one tide and the evasion of the other.

2. Salinity changes, similar to those occurring with change in tide in the inshore environment usually occupied by pink shrimp, were imposed on both postlarvae and juveniles in a constant-current apparatus.

3. Juvenile shrimp were almost invariably positively rheotactic. However, with a decrease in salinity the sign of the response was reversed, resulting in active downstream swimming. This often gave way to passive drifting.

Under conditions of low light intensity postlarvae were active in the water column, and being unable to withstand even slow currents, were easily displaced. With a decrease in salinity they sank to the substrate or remained low in the water column where they were better able to maintain position.

4. Responses of postlarvae at a discontinuity barrier between bodies of water differing in salinity indicated their ability to perceive differences as small as 1‰. There was an "aversion" to penetrating such a barrier into water of lower salinity.

5. Smaller postlarvae were more "averse" to the barrier than others approximately a week older.

6. If similar responses are elicited in nature during the flood tides, juveniles would orientate and swim against the current in an offshore direction, while postlarvae, by being active in the water column, would be displaced shoreward. Following the decrease in salinity which accompanies the ebb tide the juveniles would swim, or be passively displaced, with the current, again in an offshore direction,

and the postlarvae would sink low in the water column or settle on the substrate from where they are better able to resist displacement.

LITERATURE CITED

BEAUCHAMP, R. S. A., 1937. Rate of movement and rheotaxis in *Planaria alpina*. *J. Exp. Biol.*, **14**: 104–116.

CREUTZBERG, F., 1961. On the orientation of migrating elvers (*Anguilla vulgaris* Turt) in tidal areas. *Neth. J. Sea Res.*, **1**(3): 257–338.

GRINDLEY, J. R., 1964. Effect of low-salinity water on the vertical migration of estuarine plankton. *Nature*, **203**(4946): 781–782.

GUNTER, G., AND H. H. HILDEBRAND, 1954. The relation of total rainfall of the state and catch of marine shrimp (*Penaeus setiferus*) in Texas waters. *Bull. Mar. Sci.*, **4**(2): 95–103.

HASKINS, H., 1964. The distribution of oyster larvae. *In:* Symposium on Experimental Ecology. Occasional Publication No. 2. Narragansett Marine Lab., University of Rhode Island. Pp. 76–80.

HILDEBRAND, H. H., AND G. GUNTER, 1952. Correlation of rainfall with the Texas catch of white shrimp, *Penaeus setiferus* (Linnaeus). *Trans. Amer. Fish. Soc.*, **82**: 151–155.

HUGHES, D. A., MS. On the mechanisms underlying tide associated movements of *Penaeus duorarum*. Contribution to FAO World Scientific Conference on the Biology and Culture of Shrimps and Prawns. Mexico City, 1967.

KEENLEYSIDE, M. H. A., AND W. S. HOAR, 1954. Effects of temperature on the responses of young salmon to water currents. *Behaviour*, **7**: 77–87.

LANCE, JOAN, 1962. Effect of reduced salinity on the vertical migration of zooplankton. *J. Mar. Biol. Ass., U. K.*, **42**: 131–154.

MUNRO, J. L., A. C. JONES AND D. DIMITRIOU, MS. Abundance and distribution of the larvae of the pink shrimp (*Penaeus duorarum*) on the Tortugas shelf of Florida. Report to the U. S. Bureau of Commercial Fisheries.

SLACK-SMITH, R. J., MS. The prawn fishery of Shark Bay, Western Australia. Contribution to FAO World Scientific Conference on the Biology and Culture of Shrimps and Prawns. Mexico City, 1967.

ST. AMANT, L. S., J. G. BROOM AND T. B. FORD, 1966. Studies of the brown shrimp, *Penaeus aztecus*, in Barataria Bay, Louisiana, 1962–1965. *Proc. Gulf Carib. Fish. Inst.*, 18th Ann. Sess., Nov. 1965, pp. 1–17.

STIEVE, H., 1961. Sinnesphysiologische Betrachtungen über die Orientierung der Meerestiere bei ihren Wanderungen. *Helgolaender Wiss. Meeresunters.*, **8**(1): 153–166.

TABB, D. C., D. L. DUBROW AND A. E. JONES, 1962. Studies on the biology of the pink shrimp, *Penaeus duorarum* Burkenroad, in Everglades National Park, Florida. *Fla. St. Bd. Cons., Univ. Miami Mar. Lab., Tech. Ser.*, **37**: 1–30.

VERWEY, J., 1958. Orientation in migrating marine animals and a comparison with that of other migrants. *Arch. Néerl. Zool.*, **13**, suppl. 1, 418–445.

VERWEY, J., 1960. Über die Orientierung wandernder Meerestiere. *Helgolaender Wiss. Meeresunters.*, **7**: 51–58.